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RESEARCH ARTICLE

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River connectivity reestablished: Effects and implications of six weir removals on brown trout smolt migration

K. Birnie-Gauvin[1] | M.M. Candee[1,2] | H. Baktoft[1] | M.H. Larsen[1,3] | A. Koed[1] | K. Aarestrup[1]

[1] DTU AQUA, National Institute of Aquatic Resources, Section for Freshwater Fisheries Ecology, Technical University of Denmark, Silkeborg, Denmark

[2] Freshwater Biology, University of Copenhagen, Copenhagen, Denmark

[3] Danish Centre for Wild Salmon, Randers, Denmark

Correspondence
K. Birnie-Gauvin, DTU AQUA, National Institute of Aquatic Resources, Section for Freshwater Fisheries Ecology, Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark.
Email: kbir@aqua.dtu.dk

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Abstract

Today's river systems have been extensively modified, requiring us to rethink how we approach the management of these important ecosystems. We evaluated the effects of removing 6 weirs in River Villestrup (Jutland, Denmark) on the smolt run of brown trout (*Salmo trutta*) over the course of 12 years. During 5 of these years, we evaluated the number, size, and timing of smolts during their downstream migration. We found an increase in smolt output following the weir removals, along with a decrease in average length and indications of an earlier peak migration. Our results suggest that barrier removal has led to an increase in spawning success by adults, fry survival, recruitment, and smolt migration success. Weir removal is therefore a viable management approach to restore connectivity in freshwater streams and rivers, which promotes the passage of smolts as they migrate to marine environments.

KEYWORDS

barriers, freshwater ecosystems, migration, removal, river restoration, *Salmo trutta*, smolt

1 | INTRODUCTION

1.1 | River connectivity

The diversity, abundance, and sustainability of aquatic species have long been threatened by the human-induced fragmentation of rivers (Khan & Colbo, 2008; Saunders, Hobbs, & Margules, 1991). Barriers in the form of dams, weirs, and culverts have become so prominent in today's river systems that the majority of them have lost their original connectivity and natural characteristics (Jager, Chandler, Lepla, & Van Winkle, 2001; Jungwirth, Schmutz, & Weiss, 1998). These barriers exacerbate the current poor state of many freshwater ecosystems. Efforts to mitigate the impacts of barriers, such as fishpasses, have seen limited success (Bunt, Castro-Santos, & Haro, 2012) and are usually costly (Gibson, Haedrich, & Wernerheim, 2005). Furthermore, such approaches do not repair the damage done to the ecosystems as a whole (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017); rather, they provide an opportunity for *some* fish to move upstream or downstream past the barrier. This is particularly relevant for migratory fish species such as salmonids, which depend on freshwater migrations to complete their lifecycle (Jonsson & Jonsson, 1993; Klemetsen et al., 2003). Better management tools need to be implemented to promote the persistence of these migratory species, such as barrier removal and other types of restoration projects.

1.2 | Brown trout

The brown trout (*Salmo trutta*, Salmonidae) is a partially anadromous salmonid species, native to many regions of Europe (Jonsson & Jonsson, 1993). Brown trout spawn in the upper reaches of rivers, where the substrate is typically suitable for spawning and early growth, and predators are typically absent (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Shirvell & Dungey, 1983). Juvenile trout generally spend between 1 and 5 years in freshwater, after which individuals differentiate phenotypically (Nielsen, Aarestrup, Nørum, & Madsen, 2003). Some individuals will assume a resident phenotype and remain in freshwater their entire life, whereas others will assume the migratory phenotype and migrate to marine environments (Jonsson & Jonsson, 1993; Nielsen, Aarestrup, & Madsen, 2006). This phenomenon is known as partial migration (Chapman, Brönmark, Nilsson, & Hansson, 2011).

Although the drivers for partial migration remain poorly understood (though many hypotheses exist, Chapman et al., 2011), the benefits of migrating to sea appear to be linked to a larger availability of food items in marine environments, thus allowing migratory individuals to attain larger sizes and a greater reproductive potential (Chapman et al., 2011; Northcote, 1984; Shrimpton, 2013). Juveniles that become migratory individuals are known as smolts and differ from their resident counterparts both behaviorally and physiologically. For example, smolts appear to be less aggressive (Jonsson & Jonsson, 2011; Thorstad et al., 2012), have greater sodium-potassium ATPase activity in their gills (Aarestrup, Nielsen, & Madsen, 2000), and appear to have greater levels of blood-circulating antioxidants (Birnie-Gauvin et al., 2017).

Smolts typically migrate during the months of March to May depending on latitude (peak smolt migration period, e.g., Bohlin, Dellefors, & Faremo, 1993), though some migrate during the autumn (Winter et al., 2016 Aarestrup, Birnie-Gauvin, & Larsen, 2018). The downstream smolt migration is thought to be triggered by a range of environmental factors, such as photoperiod, temperature, and discharge (Hoar, 1988). Furthermore, smolts are thought to migrate downstream during the "smolt window." This window is thought to be affected by factors such as physiological and ecological readiness to enter marine environments, risk of predation, and growth potential (McCormick, Hansen, Quinn, & Saunders, 1998). It is thus essential that smolts be able to reach marine waters as quickly and easily as possible, with their passage unhindered.

1.3 | The restoration project

Barriers cause the upstream portion of the river to become inundated and thus can hinder the passage of smolts heading downstream due to the slowing of water (e.g., Schwinn, Aarestrup, Baktoft, & Koed, 2017) and difficulties associated with finding a safe passage route past the structure itself (e.g., Thorstad, Økland, Kroglund, & Jepsen, 2003). Furthermore, barriers hinder the upstream passage of adult trout during their spawning migration. In Denmark, such barriers often occur in the form of weirs in conjunction with fish farms. River Villestrup (northeast Jutland, Denmark) historically had 17 fish farms. In an attempt to restore the river to its original state and reinstate connectivity on the lower two thirds of the river, six weirs (five in the mainstem and one in a tributary) were removed. All associated fish farms were simultaneously closed. The weirs were likely to have been several hundred years old, though precise years of origin are not available. Each weir was originally made of concrete or wood and removed by digging and removing all parts of the structure completely. Each removal occurred within the course of a few days, though weirs were removed in different years. In 2004, when the restoration project began, seven weirs were left. The lowermost weir was removed in 2005, and five more were subsequently removed between 2010 and 2013 (see Figure 1c for weir locations and Table 1 for specific details on each weir). Today, only one weir remains in the upstream portion of the river (Figure 1c, no. 6). This study investigated the effectiveness of this restoration approach with regard to the smolt run over the course of 12 years (five study years).

2 | MATERIALS AND METHODS

2.1 | Study site and trap set up

River Villestrup is located in northeast Jutland (Denmark), where it runs for 20 km before entering the Mariager Fjord (Figure 1). The river is fed by groundwater and rainfall and has a mean annual discharge of 1.1 m^3 s^{-1}. It is home to a wild population of partially anadromous brown trout, with both resident and migratory phenotypes. Before the weir removals, river Villestrup was characterized mostly by sandy and muddy substrates in the close vicinity of the weirs, with little pool/riffle habitat. As in several Danish rivers, river Villestrup had and still has a relatively low gradient (approximately 1.0%) and meandering form. However, following the removals, the river bed is

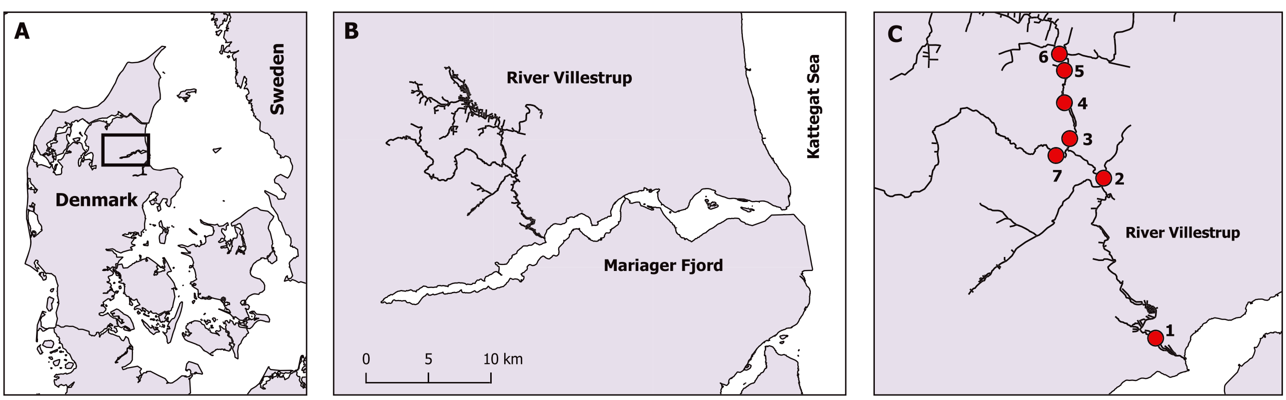

FIGURE 1 Map of River Villestrup. (a) River Villestrup is situated in north-eastern Jutland, Denmark. (b) It runs for approximately 20 km before entering the Mariager Fjord. (c) Seven weirs were present in the system originally; six were removed, with one still remaining (no. 6) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Weirs in River Villestrup

Weir no.	Height (m)	Width (m)	Length of ponded zone (m)	Fishway present?	Year of removal
1	1.9	5.9	800	Yes	2005
2	1.8	4.1	180	Yes	2012
3	0.1	5.6	0	Yes	2012
4	1.8	2.7	600	Yes	2012
5	1.5	5.0	600	Yes	2012
6	1.8	4.8	900	No	Not removed
7	1.0	1.7	500	Yes	2012

Note. Height (m), width (m), length of ponded zones (m), presence or absence of fishway, and date of removal for the weirs found in River Villestrup.

characterized by coarse, gravelly substrates. For every study year (i.e., 2004, 2008, 2009, 2015, and 2016), a full-covering Wolf trap (8-mm grid spacing; Wolf, 1951) was set up 200 m from the mouth of the river (Figure 1c, no. 1). The trap covered the entire width of the river (approximately 6 m), allowing us to capture virtually every downstream migrating fish larger than 10 cm. The trap was in place from April 1 to May 31 every year and was emptied daily during that period.

Unfortunately, given the expenses and time required to maintain a trap for 2 months, we could not perform the study continuously between 2004 and 2016. Thus, specific study years were selected to provide the most representative data to evaluate the effects of weir removal through a before-after approach.

2.2 | Fish processing

Every day during the study period, the trap was emptied to count and measure (±0.1 cm) all smolts. Fish were anaesthetised with benzocaine (0.03 g l^{-1}) for measurements and fin clipped (adipose fin). Fish were then released just downstream of the trap. Although it was unlikely, fish could return upstream after having been measured. In that case, fin-clipping allowed us to detect if a fish had already been measured and counted, and that individual was then removed from the day's count.

2.3 | Environmental variables

Water discharge data were obtained from a monitoring station located 750 m upstream of the trap. Temperature data were obtained using an underwater temperature data logger (Onset HOBO Tidbit v2 UTBI-001, range: −20°C to 70°C, Massachusetts, USA).

2.4 | Data analysis

All trout between 10.0 and 21.0 cm caught in the trap were considered to be smolts (despite coloration) for the purpose of the analysis. This is a fair assumption given the close distance between the trap and the fjord. Furthermore, a follow-up electrofishing pass downstream of the trap after the end of the smolt season showed very few trout. Mean length between years was compared using a simple linear regression model:

$$\log(\text{lenght}_i) = \text{year}_i + \varepsilon_i, \quad \varepsilon_i \sim N(0, \sigma^2). \tag{1}$$

Lengths were log-transformed to meet assumptions of normality and homoscedacity.

All statistical analyses were performed using R version 3.4.1.

3 | RESULTS

The size of the smolt run increased following the removal of weirs, with the largest class in 2015, followed by 2016 (Table 2; Figure 2). Average length of downstream migrating trout was different across study years, decreasing significantly every year ($p < .05$; Figure 3). We note an indication of earlier peak migration following weir removal (Figures 2 and 4).

4 | DISCUSSION

4.1 | Smolt run

The removal of low-head weirs in River Villestrup strongly increased smolt output. The removal of the most downstream weir in 2005 alone led to a large increase in smolts in 2008 and 2009, suggesting that reestablishing the ease of access to the fjord aided a large number of fish in successfully migrating to marine environments. Given that a Danish smolt cohort typically resides in freshwater for 1 to 2 years before migrating, the timeline of these observations are in line with the prediction that the effects of weir removal may take 2+ years to appear, though we do not have data for the years of 2006–2007 to demonstrate this. The subsequent removal of five more weirs led to an even greater increase in 2015 and 2016. Our results indicate that weir removal reinstated the natural habitat of the river, with many areas dominated by fast-moving water, riffles, and coarse substrate, where ponded zones previously were. These environmental changes presumably restored or even created new grounds ideal for spawning and early development which adults and fry did not have access to for centuries, when fish farms and mills were first established in the river system. Adult sea trout are also able to spawn farther upstream than

TABLE 2 Smolt output

	2004	2008	2009	2015	2016
Average length (cm)	16.3 ± 3.0	15.5 ± 4.2	14.5 ± 23.6	13.3 ± 2.4	13.2 ± 2.2
Average daily count	27.2	75.4	82.6	312.9	134.2
Total count	1660	4598	5038	19105	8185
Most in a day	92	931	263	5214	1853

Note. Average length of brown trout (*Salmo trutta*), average daily count, total count and most caught in a single day for each study year.

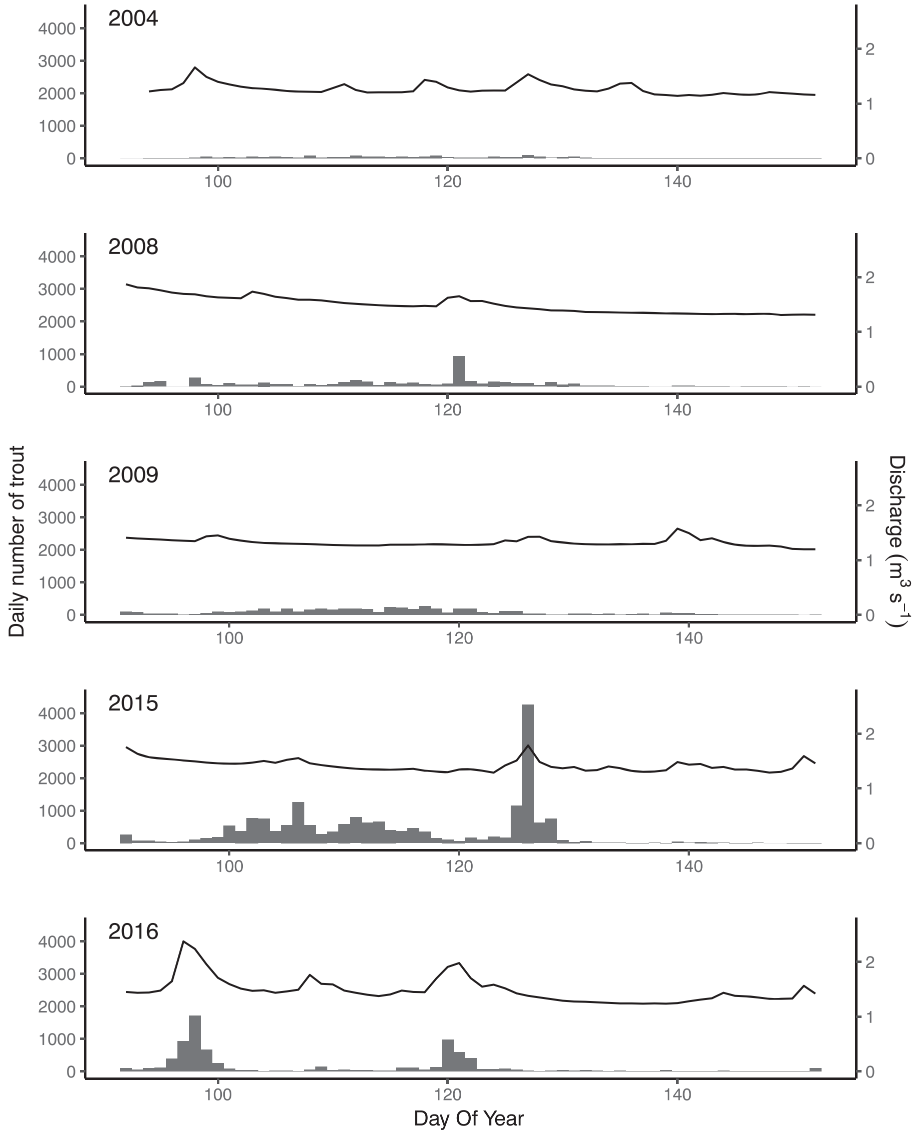

FIGURE 2 Catch per day. Number of downstream migrating brown trout (*Salmo trutta*) smolts and discharge (m^3 s^{-1}) in River Villestrup between April 1 and May 31, for years (a) 2004, (b) 2008, (c) 2009, (d) 2015, and (e) 2016.

when the barriers were present. Preliminary data shows a 9-fold increase in adult spawners between 2004 and 2016 (from an estimated 333 to 3700 individuals, data unpublished). Furthermore, observations also suggest that sedimentation caused by barriers may trap fry upon emergence (Rubin, 1998). The removal of obstacles would then also increase the survival of fry, and thus, result in a larger smolt run. Unfortunately, our set up did not allow us to follow sediment displacement post-removal, and we cannot exclude the possibility of sediments being deposited on spawning grounds. However, observations from fisheries technicians and local anglers supported an increase in the number of spawning grounds throughout the river length, with a large increase in sea trout spawners. We therefore suggest that the increase in availability of spawning grounds may have offset the negative impacts of sediment release caused by the removals. Observations of increased spawners suggest that even if sediments ended up on spawning grounds, the effects were nonproblematic.

We observed an unexpected decrease in the smolt output between 2015 and 2016. Three possible explanations arise. (1) It is possible that the large smolt run from 2015 reduced the smolt output from 2016. Previous research has shown that the density of an age class of brown trout can affect one or more subsequent age classes through intraspecific competition between cohorts (Elliott, 1994; Nordwall, Näslund, & Degerman, 2001). In this case, the 1+ age class which migrated in 2015 may have significantly reduced the abundance of the 0+ age class which would have migrated in 2016, either through predation, density-dependent mortality, or intraspecific competition (Elliott, 1994). (2) It is possible that the decrease was due to variation in the annual smolt production, which may vary from year to year due to variation in biotic and abiotic factors (Chadwick, 1982; Warren, Dunbar, & Smith, 2015). In this case, we would expect the number of smolts to increase again in the upcoming years. (3) It is possible that the population suffered high overwinter mortality due to harsh environmental conditions (Elliott, 1993). At least one other Danish stream

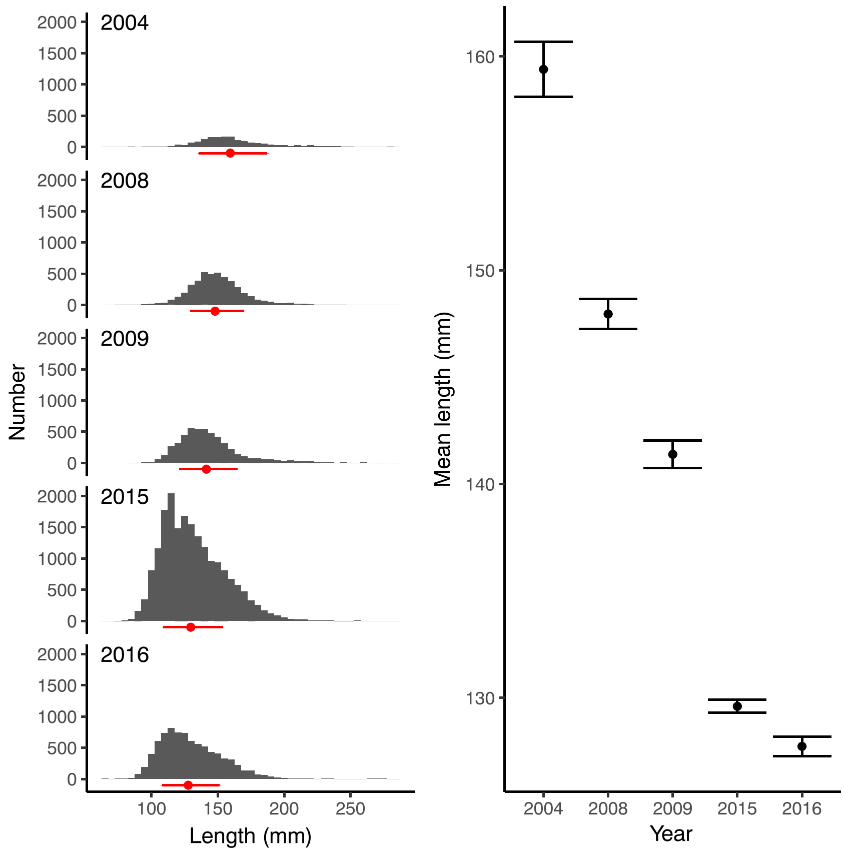

FIGURE 3 Length distribution. Left: Length distributions of downstream migrating brown trout (*Salmo trutta*). Red dots and intervals indicate mean length ± *SD*. Right: Visualization of the fitted model. Estimated mean length and associated 95% confidence intervals (back-transformed to original scale). Mean log (length) were significantly different between all years (p < .05) [Colour figure can be viewed at wileyonlinelibrary.com]

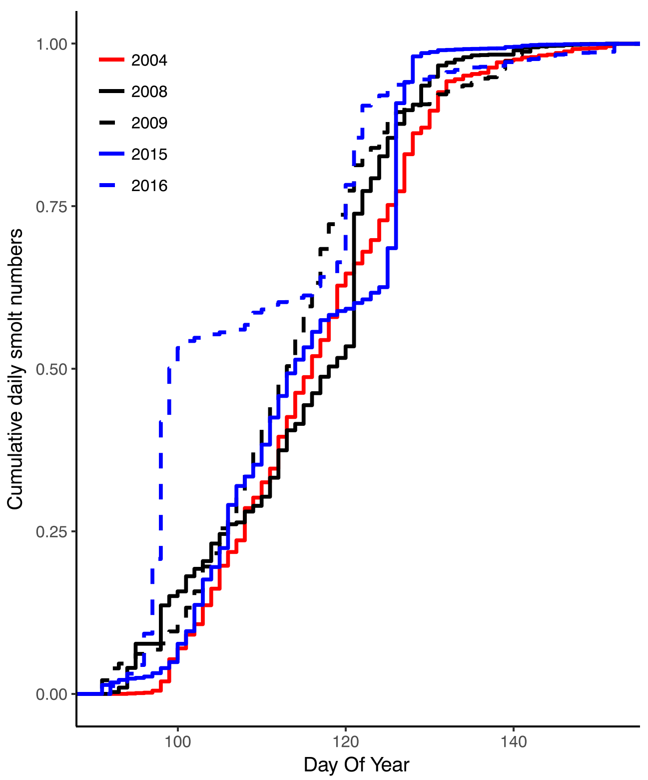

FIGURE 4 Migration timing. Cumulative migration curve for brown trout (*Salmo trutta*) smolts for each study year [Colour figure can be viewed at wileyonlinelibrary.com]

was found to have poor overwinter survival (personal observation, K. Birnie-Gauvin, Gudsø stream).

4.2 | Smolt size and peak migration

We observed a decrease in the average smolt size through the years. It is possible that following weir removal, smaller fish were also successful in migrating downstream, rather than larger fish only, which are presumably more apt at escaping predators in ponded zones or overcoming weirs (Winstone, Gee, & Varallo, 1985). In other words, smaller fish no longer get stuck at weirs and/or penetrate the grid used to prevent fish from entering the water intake channel at fish farms and are capable of descending downstream. Another possibility for progressively smaller fish following weir removal is that a greater number of fish caused higher intraspecific competition for food and may have resulted in smaller fish (Holm, Refstie, & Bø, 1990). Additionally, it is likely that spawning success and recruitment increased, which simply increased the number of migrating fish, with a wide range of sizes. Our findings likely reflect a combination of all three possible explanations. Alternatively, it is possible that the removals impacted the invertebrate community, and thus, may have reduced food availability. Although we cannot rule out this explanation, it is rather unlikely that the post-removal invertebrate community had diminished so much that fish were smaller. Because fast-flowing water is typically inhabited by different invertebrate types than slower moving water (Doisy & Rabeni, 2001), we argue that the invertebrate community *changed* rather than *diminished* post-removal.

We expected the peak migration to occur earlier following the removal of the weirs through a reduction in delays at ponded zones but cannot make that conclusion for certain. Although our results indicate a trend for an earlier peak migration, flood events during the study years make it impossible to make a meaningful analysis. Evidence suggests that dams delay the passage of migrating fish greatly (Aarestrup & Koed, 2003; Gauld, Campbell, & Lucas, 2013), and that these effects are worse when multiple dams must be overcome (Caudill et al., 2007). Ponded zones can cause smolts to lose their orientation due to diminished flow, thus delaying them (Schilt, 2007). The removal of five of the six weirs in the main stem of river Villestrup likely prevented such delays in downstream migration, thus enabling fish to reach marine environments faster.

4.3 | Implications

Our results suggest that complete barrier removal has several important implications for freshwater fisheries and river management. Weir removal presumably increases the number of adult fish able to successfully migrate upstream and spawn, perhaps due to a reduced incidence of injuries at obstacles, diminished energy expenditure to attain spawning grounds (i.e., adults no longer have to invest energy to surpass barriers), and by making impassable stretches into passable ones (Castro-Santos & Letcher, 2010). Furthermore, weir removal may increase reproductive output through successful egg emergence (i.e., unhindered by sedimentation), which would then lead to an increased recruitment rate and an increased smolt output in the following 2+ years. Weir removal also makes smolts more successful in their downstream migration via reduced mortality at fish farm intake grids (Aarestrup & Koed, 2003), reduced predation at ponded zones (Jepsen, Aarestrup, Økland, & Rasmussen, 1998), decreased delays (Aarestrup & Koed, 2003; Schilt, 2007), and presumably decreased energy expenditure. In addition, barriers may induce an artificial population structure by favoring larger individuals; removal can reinstate a more natural population structure, with a wider size range.

Many of the fish species that migrate between freshwater and marine waters, including trout, are used as indicator species for good environmental and ecological status, as they experience many habitats during their movement from upland streams to lowland rivers and then to the sea (Gough, Philipsen, Schollema, & Wanningen, 2012; Lasne, Bergerot, Lek, & Laffaille, 2007). Their importance in the context of management cannot be understated. Fish usually migrate for one of three reasons; migrations are either for spawning, feeding, or refuge seeking (Northcote, 1984). Regardless of the causes for migration, barriers diminish the ease of access to spawning and feeding grounds and hinder passage to refuge areas. These effects are likely exacerbated in rivers with numerous barriers (Lucas & Batley, 1996). Extensive fragmentation of river connectivity limits dispersal of many fish species (McLaughlin et al., 2006). Furthermore, dams impact the hydrogeomorphology of streams in some places. For example, barriers cause a decrease in water velocity, an increase in water temperature, a decrease in oxygen availability, and sedimentation (Baxter, 1977; Petts, 1984). Because most diadromous species exhibit homing behaviour, and because the latter is directly related to predictable environmental conditions such as temperature, water chemistry, and rhythmic patterns of environmental changes, their homing behavior is likely to be greatly impacted by the presence of obstacles (Lucas & Baras, 2008).

In the present study, we demonstrate that weir removal is an appropriate approach to reinstate river connectivity and to increase long-term population sustainability of fish species. We provide some of the first data evaluating the full river system effects of barrier removal and further emphasize the need to implement this approach in management schemes whenever possible.

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ORCID

K. Birnie-Gauvin http://orcid.org/0000-0001-9242-0560

H. Baktoft http://orcid.org/0000-0002-3644-4960

REFERENCES

Aarestrup, K., Birnie-Gauvin, K., & Larsen, M. H. (2018). Another paradigm lost? Autumn downstream migration of juvenile brown trout: Evidence for a presmolt migration. *Ecology of Freshwater Fish*, *27*, 513–516.

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*, 169–176.

Aarestrup, K., Nielsen, C., & Madsen, S. S. (2000). Relationship between gill Na+, K+-ATPase activity and downstream movement in domesticated and first-generation offspring of wild anadromous brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 2086–2095.

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M., & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research*, *62*, 143–170.

Baxter, R. M. (1977). Environmental effects of dams and impoundments. *Annual Review of Ecology and Systematics*, *8*, 255–283.

Birnie-Gauvin, K., Aarestrup, K., Riis, T. M. O., Jepsen, N., & Koed, A. (2017). Shining the light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers and its implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 1345–1349.

Birnie-Gauvin, K., Peiman, K. S., Larsen, M. H., Baktoft, H., Aarestrup, K., Willmore, W. G., & Cooke, S. J. (2017). Oxidative stress and partial migration in brown trout (*Salmo trutta*). *Canadian Journal of Zoology*, *95*, 829–835.

Bohlin, T., Dellefors, C., & Faremo, U. (1993). Timing of sea-run brown trout (Salmo trutta) smolt migration: Effects of climatic variation. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 1132–1136.

Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*, 457–478.

Castro-Santos, T., & Letcher, B. H. (2010). Modeling migratory energetics of Connecticut River American shad (Alosa sapidissima): Implications for the conservation of an iteroparous anadromous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 806–830.

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., … Peery, C. A. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: Delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 979–995.

Chadwick, E. M. P. (1982). Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 1496–1501.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*, 1764–1775.

Doisy, K. E., & Rabeni, C. F. (2001). Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society*, *20*, 17–32.

Elliott, J. M. (1993). A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. In R. J. Gibson, & R. E. Cutting (Eds.), *Production of juvenile Atlantic salmon, Salmo salar, in natural waters* (pp. 109–122). Ottawa: Canadian Special Publication of Fisheries and Aquatic Sciences.

Elliott, J. M. (1994). *Quantitative ecology and the brown trout*. Oxford: Oxford University Press.

Gauld, N. R., Campbell, R. N. B., & Lucas, M. C. (2013). Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. *Science of the Total Environment*, *458*, 435–443.

Gibson, R. J., Haedrich, R. L., & Wernerheim, C. M. (2005). Loss of fish habitat as a consequence of inappropriately constructed stream crossings. *Fisheries*, *30*, 10–17.

Gough, P., Philipsen, P., Schollema, P.P. & Wanningen, H. (2012). From sea to source. International guidance for the restoration of fish migration highways. Regional Water Authority Hunze en Aa's, Netherlansds.

Hoar, W.S. (1988). The physiology of smolting salmonids. *Fish Physiology*, 11, 275–343.

Holm, J. C., Refstie, T., & Bø, S. (1990). The effect of fish density and feeding regimes on individual growth rate and mortality in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, *89*, 225–232.

Jager, H. I., Chandler, J. A., Lepla, K. B., & Van Winkle, W. (2001). A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes*, *60*, 347–361.

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radiotagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, *371*, 347–353.

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, *3*, 348–365.

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout: Habitat as a template 355 for life histories*. Dordrecht: Springer.

Jungwirth, M., Schmutz, S., & Weiss, S. (1998). *Fish migration and fish bypasses*. Oxford: Fishing News Books.

Khan, B., & Colbo, M. H. (2008). The impact of physical disturbance on stream communities: Lessons from road culverts. *Hydrobiologia*, *600*, 229–235.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*, 1–s.

Lasne, E., Bergerot, B., Lek, S., & Laffaille, P. (2007). Fish zonation and indicator species for the evaluation of the ecological status of rivers: Example of the Loire basin (France). *River Research and Applications*, *23*, 877–890.

Lucas, M., & Baras, E. (2008). *Migration of freshwater fishes*. Oxford: Blackwell-Science.

Lucas, M. C., & Batley, E. (1996). Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: Implications for river management. *Journal of Applied Ecology*, *33*, 1345–1358.

McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 77–92.

McLaughlin, R. L., Porto, L., Noakes, D. L., Baylis, J. R., Carl, L. M., Dodd, H. R., … Randall, R. G. (2006). Effects of low-head barriers on stream fishes: Taxonomic affiliations and morphological correlates of sensitive species. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 766–779.

Nielsen, C., Aarestrup, K., & Madsen, S. S. (2006). Comparison of physiological smolt status in descending and nondescending wild brown trout (*Salmo trutta*) in a Danish stream. *Ecology of Freshwater Fish*, *15*, 229–236.

Nielsen, C., Aarestrup, K., Nørum, U., & Madsen, S. S. (2003). Pre-migratory differentiation of wild brown trout into migrant and resident individuals. *Journal of Fish Biology*, *63*, 1184–1196.

Nordwall, F., Näslund, I., & Degerman, E. (2001). Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 2298–2308.

Northcote, T. G. (1984). Mechanisms of fish migration in rivers. In J. D. McCleave, G. P. Arnold, J. J. Dodson, & W. H. Neill (Eds.), *Mechanisms of migration in fishes* (pp. 317–355). New York: Springer.

Petts, G. E. (1984). *Impounded rivers: Perspectives for ecological management*. Chichester: John Wiley.

Rubin, J. F. (1998). Survival and emergence pattern of sea trout fry in substrata of different compositions. *Journal of Fish Biology*, *53*, 84–92.

Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: A review. *Conservation Biology*, *5*, 18–32.

Schilt, C. R. (2007). Developing fish passage and protection at hydropower dams. *Applied Animal Behaviour Science*, *104*, 295–325.

Schwinn, M., Aarestrup, K., Baktoft, H., & Koed, A. (2017). Survival of migrating sea trout (*Salmo trutta*) smolts during their passage of an artificial lake in a Danish lowland stream. *River Research and Applications*, *33*, 558–566.

Shirvell, C. S., & Dungey, R. G. (1983). Microhabitats chosen by brown trout for feeding and spawning in rivers. *Transactions of the American Fisheries Society*, *112*, 355–367.

Shrimpton, J. M. (2013). Seawater to freshwater transitions in diadromous fishes. In S. D. McCormick, & C. J. Brauner (Eds.), *Fish physiology: Euryhaline fishes* (pp. 327–393). Oxford: Academic Press.

Thorstad, E. B., Økland, F., Kroglund, F., & Jepsen, N. (2003). Upstream migration of Atlantic salmon at a power station on the River Nidelva, Southern Norway. *Fisheries Management and Ecology*, *10*, 139–146.

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*, 500–542.

Warren, M., Dunbar, M. J., & Smith, C. (2015). River flow as a determinant of salmonid distribution and abundance: A review. *Environmental Biology of Fishes*, *98*, 1695–1717.

Winter, E. R., Tummers, J. S., Aarestrup, K., Baktoft, H., & Lucas, M. C. (2016). Investigating the phenology of seaward migration of juvenile brown trout (Salmo trutta) in two European populations. *Hydrobiologia*, *775*(1), 139–151.

Winstone, A. J., Gee, A. S., & Varallo, P. V. (1985). The assessment of flow characteristics at certain weirs in relation to the upstream movement of migratory salmonids. *Journal of Fish Biology*, *27*, 75–83.

Wolf, P. (1951). A trap for the capture of fish and other organisms moving downstream. *Transactions of the American Fisheries Society*, *80*, 41–45.

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